

Graph theoretic approach to parallel gene assembly

Tero Harju^a, Chang Li^b, Ion Petre^{c,b,*}

^a *Department of Mathematics, University of Turku, Turku Centre for Computer Science, FIN-20014 Turku, Finland*

^b *Department of IT, Åbo Akademi University, Turku Centre for Computer Science, FIN-20520 Turku, Finland*

^c *Academy of Finland, Finland*

Received 23 August 2007; received in revised form 22 January 2008; accepted 24 January 2008

Available online 3 March 2008

Abstract

We study parallel complexity of signed graphs motivated by the highly complex genetic recombination processes in ciliates. The molecular gene assembly operations have been modeled by operations of signed graphs, i.e., graphs where the vertices have a sign + or −. In the optimization problem for signed graphs one wishes to find the parallel complexity by which the graphs can be reduced to the empty graph. We relate parallel complexity to matchings in graphs for some natural graph classes, especially bipartite graphs. It is shown, for instance, that a bipartite graph G has parallel complexity one if and only if G has a unique perfect matching. We also formulate some open problems of this research topic.

© 2008 Elsevier B.V. All rights reserved.

Keywords: Gene assembly; Signed graphs; Parallel assembly; Local complement; Split graphs; Double-split graphs; Perfect matching

1. Introduction

In this paper we take a graph theoretic approach to gene assembly of ciliates. After shortly introducing the biological motivation of the topic, we study the model of gene assembly in terms of signed graphs and their operations. Our main problems concern low parallel complexity of these operations on signed graphs which are undirected graphs with vertices having a sign + or −. We consider three basic operations (negative, positive and double rules) on signed graphs that correspond to the gene assembly operations in the genetic transformation process in ciliates. Each signed graph can be reduced to the empty graph using a sequence of these operations. However, some of the operations may be applicable simultaneously to a signed graph, which raises the question of parallel complexity of the graphs: how many parallel steps are needed in the reduction to the empty graph.

We relate parallel complexity to matchings in graphs for some natural graph classes, especially bipartite graphs. We show for instance, that a (unsigned) bipartite graph G can be reduced to the empty graph in one parallel step if and only if G has a unique perfect matching. We also show that all trees with positive signs on the vertices can be reduced in one step to a graph with negative signs on the vertices. We believe that some of the results have independent interest from a purely graph theoretic point of view; see e.g. Lemma 8.6.

* Corresponding author. Fax: +358 22154732.

E-mail addresses: harju@utu.fi (T. Harju), lchang@abo.fi (C. Li), ipetre@abo.fi (I. Petre).

It is interesting to note that the operations *gpr* and *gdr* correspond to the graph operations defined by Bouchet [1,2] in the context of circle graphs. The focus of the present article is different from that in [1,2].

A visible part of the present paper consists of open problems of this research topic.

2. Preliminaries

2.1. Biological motivation

Ciliates are ancient, eucaryotic single-celled organisms [5], that inhabit practically all types of aqueous environments. The most striking feature, common to all species of ciliates, is that they possess two dissimilar nuclei, micronucleus and macronucleus, which have different functions in the cell. The macronucleus comprises the household genome carrying the RNA transcription needed for cell growth and proliferation [19]. It consists of short gene-size chromosomes [20], and it is generated from the micronucleus after cell mating. The micronucleus, on the other hand, is active during cell mating when DNA material is exchanged between two cells. It has no known function in the normal life of the cell. The micronuclear genes are located in long chromosomes where each gene can be fragmented in several segments known as macronuclear destined sequences (MDSs). The MDSs are separated by, often quite long, non-coding segments (internally eliminated segments, IESs), and, moreover, the MDSs may occur in permuted order and some of them even inverted.

The process of converting micronucleus to macronucleus involves massive DNA rearrangement with respect to the genomic difference of the two nuclei [16]. During the macronucleus development all spacer sequences (IESs) between MDSs are excised and the remaining MDSs are recombined in correct order to form the genes. This process is referred to as *gene assembly*. From computational point of view, MDSs are arranged as the *linked list* data structure, where the outgoing pointer of one data matches with the incoming pointer of the next data. Thus, the double occurred sequences at IES/MDS junctions can be referred to as *pointers*, and the whole process may be seen as pointer-guided [10].

Concerning how IESs are recognized/excised and how MDSs are unscrambled/recombined, several models have been postulated [17,18,22]. In this paper, we consider the intramolecular model [7], where three molecular operations are postulated [21]: loop recombination, hairpin recombination and double-loop recombination. In each of these operations, the molecule folds on itself so that two or more pointers get aligned and through recombination two or more MDSs get combined into a bigger composite MDS. The process continues until all MDSs have been assembled.

In the intramolecular model, the MDSs arrangement on a micronuclear gene is formalized on three levels of abstraction [6]: *MDS descriptors* (denoting the sequence of the incoming pointers and outgoing pointers of MDSs), *legal strings* (denoting the sequence and polarity of the double-occurred pointers), and *signed graphs* (denoting the overlap relation between the pointers and the pointer polarity). Correspondingly, the three molecular operations are formalized as the reduction of MDSs pointers, strings and graphs.

In this paper we concentrate on the graph theoretic approach on gene assembly. The basic problem is to find parallel gene assembly strategies for a given signed graph associated with a micronuclear gene pattern, and to give an optimal parallel assembly strategy that requires the least assembly steps.

Our first problem is: when can multiple operations form a single step of an assembly strategy? On the molecular level, we can see that the MDSs whose pointers do not occur on the overlapping repeats can be assembled in parallel. On the graph level, we do not have a full characterization of applying multiple assembly operations in parallel. The second problem is: in how many steps can any given gene pattern be assembled? For signed graphs, this problem concerns the upper bounds on the number of reduction steps. It turns out that this bound does not completely correspond to the number of pointers in the gene patterns, but it depends on the type of graph and the reduction strategy that has been applied.

In this paper, we investigate these two problems on various signed graphs, e.g., bipartite and tripartite graphs, trees, and also arbitrary graphs. For some types of graphs we prove that the number of parallel reduction steps is bounded.

2.2. Signed graphs

In this section we introduce basic notions concerning signed graphs and the reduction operations for signed graphs. Let $G = (V, E)$ be a finite undirected graph without self loops or multiple edges. The number $|V|$ of the vertices, is called the *order* of G . For simplicity, we write $v \in G$ if v is a vertex, and $e \in E(G)$, if e is an edge of G .

The *neighborhood* of a vertex v is $N_G(v) = \{u \mid \{v, u\} \in G\}$. We call the set $N_G^*(v) = N_G(v) \cup \{v\}$ the *closed neighborhood* of v . We say that two vertices u, v are *twins* if $N_G^*(u) = N_G^*(v)$. The vertex v is *isolated* if $N_G(v) = \emptyset$. A vertex v is a *leaf*, if it has exactly one neighbor. We call G *discrete* if all its vertices are isolated. A subset $A \subseteq G$ is *stable*, if there are no edges $\{v, u\}$ with $v, u \in A$. A graph G is called a *clique* (or a *complete graph*) if any two vertices in G are adjacent.

A subset $M \subseteq E(G)$ is a *matching* of a graph G if no two edges in M have a common end point. A matching M is said to be *perfect*, if each vertex is an endpoint of an edge in M . A matching M is *maximal* if $M \cup \{e\}$ is not a matching for all edges $e \notin M$, and M is *maximum matching*, if its cardinality is the largest possible.

A *signed graph* $G = (V, E, \sigma)$ consists of a graph (V, E) together with a labeling function $\sigma: V \rightarrow \{+, -\}$ of the vertices. (A signed graph is often called a *marked graph* in literature.) A vertex $v \in G$ is said to be *positive* (*negative*, resp.) if $\sigma(v) = +$ ($\sigma(v) = -$, resp.). We let

$$G^+ = \{v \mid \sigma(v) = +\} \text{ and } G^- = \{v \mid \sigma(v) = -\}$$

the corresponding sets of positive and negative vertices in G . We say that a signed graph is a *negative graph* (a *positive graph*, resp.) if all its vertices are negative (positive, resp.). Also, an edge $e = \{v, u\}$ is called *negative*, if $v, u \in G^-$.

Let $G = (V, E, \sigma)$ be a signed graph. For each $A \subseteq G$, let $G - A$ denote the subgraph induced by the set of vertices $V \setminus A$.

Denote by $\text{loc}_v(G)$ the *local complement* of G at v : $\text{loc}_v(G) = (V, E', \sigma')$, where

$$\{x, y\} \in E' \iff \begin{cases} \{x, y\} \notin E & \text{and } x, y \in N_G(v), \quad \text{or} \\ \{x, y\} \in E & \text{and } x \notin N_G(v) \quad \text{or } y \notin N_G(v). \end{cases}$$

Also, $\sigma'(x) = +$ if and only if $\sigma(x) = -$, for all $x \in N_G(v)$ and $\sigma'(x) = \sigma(x)$, otherwise.

A *split graph* is a graph G in which the vertex set can be partitioned into two sets K and A such that K induces a clique and A induces a stable set in G .

We say that $G = (V, E)$ is a *double-split graph* if the vertex set can be partitioned into four sets $A = \{a_1, \dots, a_m\}$, $B = \{b_1, \dots, b_m\}$, $C = \{c_1, \dots, c_n\}$, $D = \{d_1, \dots, d_n\}$ for some $m, n \geq 2$ such that:

- A and B are stable sets in G ;
- C and D are cliques in G ;
- $\{a_i, b_i\} \in E$ for $1 \leq i \leq m$ and $\{c_j, d_j\} \notin E$ for $1 \leq j \leq n$;
- $\{a_i, b_j\} \notin E$ for $i \neq j$ and $\{c_i, d_j\} \in E$ for $i \neq j$;
- for each $1 \leq i \leq m$ and $1 \leq j \leq n$, either $\{a_i, c_j\} \in E$ and $\{b_i, d_j\} \in E$ or $\{a_i, d_j\} \in E$ and $\{b_i, c_j\} \in E$.

For two signed graphs G and H on disjoint vertex sets, say $V(G)$ and $V(H)$, let $G \oplus H$ be their *disjoint union*, i.e., the vertex set of $G \oplus H$ is $V(G) \cup V(H)$, and its edges form the set

$$E(G \oplus H) = E(G) \cup E(H).$$

The *complete connection* $G \otimes H$ has the vertex set $V(G) \cup V(H)$ and the edge set is

$$E(G \otimes H) = E(G) \cup E(H) \cup \{\{v, u\} \mid v \in G, u \in H\}.$$

2.3. Graph reduction rules

The three molecular operations are formalized as reduction rules for signed graphs as follows. For details on how the molecular operations are translated to these formal operations, we refer to [6].

Let v and u be two vertices.

- The (*graph*) *negative rule* for v is applicable to G if $v \in G^-$ and it is isolated in G . The result is the signed graph $\text{gnr}_v(G) = G - v$. The *domain* of gnr_v is $\text{dom}(\text{gnr}_v) = \{v\}$.
- The (*graph*) *positive rule* for v is applicable to G if $v \in G^+$. The result is the signed graph $\text{gpr}_v(G) = \text{loc}_v(G) - \{v\}$. The *domain* of gpr_v is $\text{dom}(\text{gpr}_v) = \{v\}$.

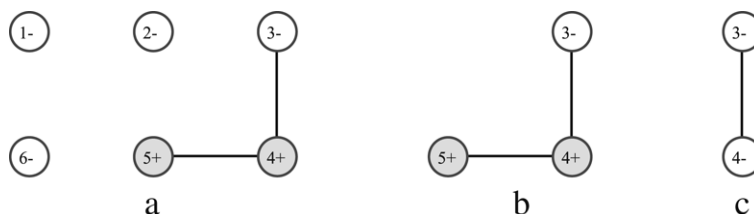


Fig. 1. (a) A signed graph G . (b) Applying gnr_2 , gnr_3 and gnr_7 to G , reduces all the isolated negative vertices. (c) Further applying gpr_6 reduces the graph to a negative edge of $\{4, 5\}$, where $\text{gdr}_{4,5}$ is applicable.

- The (graph) double rule for $v \neq u$ is applicable to G if $v, u \in G^-$ and $e = \{v, u\} \in E(G)$. The result is the signed graph $\text{gdr}_e(G) = (G \setminus \{v, u\}, E', \sigma')$ where σ' equals σ restricted to $G - \{v, u\}$, and E' is obtained from E by complementing the edges that join vertices of $N_G(v)$ and $N_G(u)$. This means that the status of a pair $\{x, y\}$ as an edge will change if and only if v and u belong to different sets $N_G(v) \setminus N_G(u)$, $N_G(u) \setminus N_G(v)$, $N_G(v) \cap N_G(u)$. The domain of gdr_e is $\text{dom}(\text{gdr}_e) = \{v, u\}$.

We let $\text{Op} = \{\text{gnr}_v, \text{gpr}_v, \text{gdr}_{v,u} \mid v \neq u\}$ denote the full set of the operations.

Let G be a signed graph. A composition $\varphi = \varphi_n \circ \dots \circ \varphi_1$ of operations $\varphi_1, \dots, \varphi_n \in \text{Op}$ is called a *graph reduction* for G if φ is applicable to G . We say that φ is a *successful reduction strategy* for G if $\varphi(G) = \emptyset$.

Example 1. Consider the signed graph G of six vertices shown in Fig. 1(a). One successful reduction strategy of G is: $\varphi = \text{gdr}_{4,5} \circ \text{gpr}_6 \circ \text{gnr}_7 \circ \text{gnr}_3 \circ \text{gnr}_2$, see Fig. 1(b) and (c).

3. Parallelism

Intuitively, a set of operations can be applied in parallel if and only if each application is independent of the others. In other words, a number of operations can be applied in parallel to a signed graph if they can be (sequentially) applied in any order to that graph. Note that this is consistent with how parallelism and concurrency are defined in Computer Science. The following gives the definition of parallel application of the three molecular operations on a signed graph.

Definition 1. Let $S \subseteq \text{Op}$ be a set of k rules and let G be a signed graph. We say that the rules in S can be applied in parallel to G if for any ordering $\varphi_1, \varphi_2, \dots, \varphi_k$ of S , the composition $\varphi_k \circ \dots \circ \varphi_1$ is applicable to G .

Based on the definition of parallelism, which presumes that the rules are applicable in any possible order, the following theorem shows that the result is always the same regardless of the order in which they are applied.

Theorem 3.1 ([11]). Let G be a signed graph and let $S \subseteq \text{Op}$ be a set of operations applicable in parallel to G . Then for any two compositions φ and ψ of the operations of S , $\varphi(G) = \psi(G)$.

Based on Theorem 3.1, we can write $S(G) = \varphi(G)$ for any set S of operations applicable in parallel to G and any composition φ of these operations. We define the parallel complexity as follows.

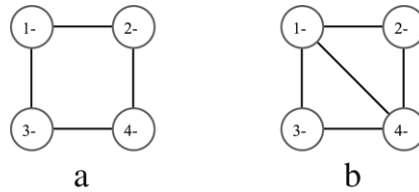
Definition 2 ([13]). Let G be a signed graph, and let $S_1, \dots, S_k \subseteq \text{Op}$ be sets of operations each applicable in parallel to G . If $(S_k \circ \dots \circ S_1)(G) = \emptyset$, then we say that $S = S_k \circ \dots \circ S_1$ is a *parallel reduction strategy* for G . In this case the *parallel complexity* of S is $\mathcal{C}(S) = k$. The parallel complexity of the signed graph G is:

$$\mathcal{C}(G) = \min\{\mathcal{C}(S) \mid S \text{ is a parallel reduction strategy for } G\}.$$

We denote the *square* C_4 and *diamond* D_4 as the negative graphs shown in Fig. 2. In both graphs, no two edges can be reduced in parallel.

The following provides a simple criterion for two rules to be applicable in parallel.

Theorem 3.2 ([12]). Let G be a signed graph and let $\varphi, \psi \in \text{Op}$ be two rules applicable to G such that $\text{dom}(\varphi) \cap \text{dom}(\psi) = \emptyset$.

Fig. 2. (a) The square C_4 ; (b) the diamond D_4 .

- (i) If $\varphi = \text{gnr}_v$ is a negative rule, then φ and ψ can be applied in parallel to G .
- (ii) If $\varphi = \text{gpr}_v$ is a positive rule, then φ and ψ can be applied in parallel to G if and only if $N_G(v) \cap \text{dom}(\psi) = \emptyset$.
- (iii) Two double rules φ and ψ can be applied in parallel to G if and only if the subgraph of G induced by $\text{dom}(\varphi) \cup \text{dom}(\psi)$ is not isomorphic to C_4 or D_4 .

The problem of finding a maximum size set of double operations that can be applied in parallel to a given set of negative edges in a given signed graph G remains open. This is related to the following problem.

Problem 1. For a given graph G and a given set of negative edges A , decide efficiently whether $\text{gdr}_A = \{\text{gdr}_e \mid e \in A\}$ is applicable in parallel to G .

4. A bound on the parallel complexity

The main open problem of this study is whether the parallel complexity of signed graphs is finitely bounded, i.e., for each positive integer n , does there exist a signed graph with parallel complexity $\mathcal{C}(G) \geq n$?

For some types of graphs, an upper bound for parallel complexity is easy to obtain, the following are some of the examples.

Example 2. (a) For a discrete signed graph G , $\mathcal{C}(G) = 1$.

(b) For a signed clique G , $\mathcal{C}(G) \leq 2$. Indeed, if there exists a positive vertex $v \in G^+$, then $\text{gpr}_v(G)$ is discrete, and then one can apply in parallel the rules gpr_u or gnr_u for each remaining vertex u . On the other hand, if $G^+ = \emptyset$, then choose a maximal matching M of the edges of the clique. Observe that, for any $e \in M$, the graph $\text{gdr}_e(G)$ is a smaller clique, and hence $M \setminus \{e\}$ is applicable to $\text{gdr}_e(G)$. It follows that $\text{gdr}_M = \{\text{gdr}_e \mid e \in A\}$ can be applied in parallel to G , and this results in the empty graph or a singleton graph depending on whether the clique G has even or odd order.

(c) Let G be a negative complete bipartite graph, i.e., $G = S_1 \otimes S_2$ for two discrete graphs S_1 and S_2 . Then $\mathcal{C}(G) \leq 2$. Indeed, for any $e \in E(G)$, $\text{gdr}_e(G)$ is either a discrete graph or it is empty (in case G has exactly one edge).

The following lemma for double rules gdr_e is needed in Theorem 4.4.

Lemma 4.1. Let G be a signed graph. Then G has no parallel applications of two double rules if and only if $G^- = (H \otimes S_1) \oplus S_2$, where H is a complete bipartite graph, and S_1 and S_2 are (possibly empty) discrete graphs.

Proof. We assume without loss of generality that the graph G is negative.

For the direct implication, note that the result holds for graphs with up to 4 vertices. Especially, the square C_4 and the diamond D_4 can be represented in the required form, but, for instance the clique K_4 on four vertices cannot. Consider a larger graph and note that in that graph there can be several isolated vertices, but it can have only one non-trivial connected component. We remove the isolated vertices and thus assume without loss of generality that the graph is connected.

We claim that for any $v, u \in G$, if $\{v, u\} \notin E(G)$ then $N(v) = N(u)$. For this, assume there exists a vertex $a \in N(v) \setminus N(u)$. Since G is connected, there exists a vertex $b \in N(u)$. Now, the set $\{v, u, a, b\}$ induces a subgraph different from C_4 and D_4 and so, $\text{gdr}_{v,a}$ and $\text{gdr}_{u,b}$ are both applicable to G . This proves the present claim.

Let S_1 be a maximal stable subset of G . Hence each vertex $v \notin S_1$ is adjacent to a vertex in S_1 , and, by the claim, S_1 and $W = G \setminus S_1$ are completely connected. Since G has no cliques K_4 on four vertices, W does not have triangles K_3 and thus no subgraphs D_4 . Therefore all four element induced subgraphs in W are isomorphic to the square C_4 . This is possible only if W induces a complete bipartite subgraph H . Hence $G = H \otimes S_1$ as required.

The reverse implication is clearly true. \square

In a complete tripartite graph H the vertex set is partitioned to three subsets A_1, A_2, A_3 and a pair $\{v, u\}$ is an edge if and only if $v \in A_i$ and $u \in A_j$ for $i \neq j$.

Corollary 4.2. *A signed graph G has no parallel applications of two double rules if and only if G^- consists of a discrete graph and a complete tripartite graph, where some of the three components can also be empty. Moreover, in this case, if G is negative, then $\mathcal{C}(G) \leq 2$.*

Proof. In Lemma 4.1, $H \otimes S_1$ is a complete tripartite graph. For the last claim for negative G , applying gdr_e for one edge $e \in E(G)$ results in a discrete graph, which reduces to the empty graph in one step. \square

Theorem 4.3. *Let G be a negative graph with n vertices. Then $\mathcal{C}(G) \leq n/4 + 2$.*

Proof. If no double rule is applicable to G , then G is discrete and thus $\mathcal{C}(G) = 1$. If at least two double rules gdr_e and gdr_f are applicable in parallel to G , then the order of G is decreased by at least 4 in one step. Consider then the case, where exactly one gdr -rule is applicable to G . By Corollary 4.2, $G = H \oplus S$, with H a complete tripartite graph and S a discrete graph. Here $\mathcal{C}(G) = \mathcal{C}(H) \leq 2$, since for each edge $e \in H$, the graph $\text{gdr}_e(H)$ is discrete. \square

In the next we give a non-finite upper bound for signed graphs in general.

Theorem 4.4. *Let G be a signed graph with n vertices. Then $\mathcal{C}(G) \leq n/2 + 4$.*

Proof. We show that there is a reduction of each signed graph of $n \geq 4$ vertices which reduces the graph by two vertices in one step or four vertices in two steps. Assume that the only applicable rule to G is a gpr . In particular, G must be connected. Since no double rule gdr_e is applicable, the negative vertices G^- form a stable set, and since at most one positive rule gpr_v is applicable, the positive vertices G^+ form a clique.

Consider a positive vertex $v \in G^+$ of minimum degree $|N_G(v)|$, and let

$$A = G^+ \setminus \{v\}, \quad B = N_G(v) \cap G^-, \quad \text{and} \quad C = G^- \setminus B.$$

Hence $A \cup \{v\}$ forms a clique and $B \cup C$ is a stable set in G . We can assume that $A \neq \emptyset$, for otherwise also $C = \emptyset$ and one quickly sees that $\mathcal{C}(G) \leq 3$. Let $G_v = \text{gpr}_v(G)$. Then A and C induce negative discrete graphs in G_v , B induces a positive clique, and there are no edges between B and C in G_v .

We can assume that $B \neq \emptyset$, since otherwise G_v is a negative connected graph, and, by Theorem 4.3, $\mathcal{C}(G) \leq \mathcal{C}(G_v) + 1 \leq (n-1)/4 + 3 < n/2 + 4$.

(1) Let $a \in A$ be such that $\{a, c\} \notin E(G)$ for all $c \in C$. By the minimality assumption on v , we have $B \subseteq N_G(a)$, and therefore a is isolated in G_v .

Notice that if $C = \emptyset$ then this case holds for all $a \in A$, and then G_v consists of a positive clique and a set of isolated vertices. In this case one easily sees that $\mathcal{C}(G_v) \leq 2$, and hence $\mathcal{C}(G) \leq 3$.

Assume thus that $C \neq \emptyset$.

(2) Let $a \in A$ be such that $\{a, c\} \in E(G)$ for some $c \in C$. Then $\{a, c\} \in E(G_v)$ with $a, c \in G_v^-$, and if $\{a, b\} \in E(G)$ for any $b \in B$ then $\{a, b\} \notin E(G_a)$, and $\text{gdr}_{a,c}$ and gpr_b can be applied in parallel to G_v giving a reduction of four vertices in two steps. Also, if there exists a vertex $u \in A$ as in the above case (1) where u becomes isolated in G_v , then $\text{gdr}_{a,c}$ and gpr_u can be applied in parallel to G_v . Therefore we can assume that $\{a, b\} \notin E(G)$ for all $a \in A$ and $b \in B$. By connectivity, each $x \in C$ is adjacent to at least one vertex in A , and not adjacent to any other vertices. Thus $\{a, x\} \in E(G)$ for all $x \in C$, or we have two parallel applications of the double rule by Theorem 3.2(iii). In conclusion, we have in G :

$$N_G(v) \setminus A = B, \quad N_G(a) \setminus A = C \cup \{v\} \quad \text{for each } a \in A, \quad B \cup C \text{ is a stable set.}$$

In this case, $\mathcal{C}(G) \leq 4$. Indeed, the first step of such a strategy for G applies rule gpr_a for some $a \in A$. Then, in $\text{gpr}_a(G)$, both $A' = (A \setminus \{a\}) \cup \{v\}$ and B induce negative discrete graphs, C induces a positive clique, and $N_{G_a}(v) = B \cup C$. Applying once gdr_e for an edge $e = vb$ with $b \in B$ gives a disjoint union of a discrete graph and a positive clique C . Such a graph can be easily reduced in two steps to the empty graph. \square

We formulate the main open problem of this area, in three different setups.

Problem 2. Does there exist a constant k such that $\mathcal{C}(G) \leq k$ whenever G is (a) a signed tree, (b) a negative graph, (c) any signed graph?

5. Graphs avoiding one type of operations

A step towards solving [Problem 2](#) is performed by an attempt to find high complexity graphs that avoid one basic type of rule, either gnr , or gpr , or gdr , in all reduction strategies. The approach is clear for the double rule: since gdr removes two vertices with every application, avoiding gdr -rules in all strategies may lengthen the reduction strategies. We investigate this problem in the following, for all three operations.

Perhaps unexpectedly, determining whether all reduction strategies of a signed graph G avoid the negative rule turns out to be a difficult problem. Recall that a negative rule gnr_v simply removes the negative isolated vertex v . The signed graphs that have no reductions using the gnr -rules are those that can be reduced using only gpr and gdr , for which a string-based characterization was given in [3], see also [8], but giving a graph-based characterization remains an open problem.

Problem 3. Give a characterization of the graphs that avoid the negative rules in all reduction strategies.

On the other hand, the case of the positive rules has a simple characterization shown in the next lemma.

Lemma 5.1. *A signed graph G has no reductions using any positive rules gpr_v if and only if G is negative.*

Proof. If a signed graph G has a positive vertex v , it can be removed only by gpr_v or its sign is changed to negative by another positive rule gpr_u . \square

Let us consider now the case of gdr .

Lemma 5.2. *Let G be a connected signed graph with no reduction using a double rule. Then $G = G^+ \otimes G^-$, where G^+ is either a clique, or a disjoint union of two cliques, and G^- is discrete. In this case, $\mathcal{C}(G) \leq 3$.*

In the above, we allow $G^- = \emptyset$, in which case G is an positive clique. The conclusion can be rewritten in the form $G = (K \oplus K') \otimes S$, where K, K' are positive cliques and S is a negative discrete graph, where we allow that K, K' , and S can be empty.

Proof of the Lemma. If there is an induced path P_3 of three vertices in G^+ , then by applying gpr_v to the middle vertex v , we obtain a negative edge e , and so gdr_e can be applied to $\text{gpr}_v(G)$; a contradiction. Obviously, if a connected graph does not have an induced path P_3 , then it is a clique. Therefore, G^+ is a disjoint union of cliques, say $G^+ = G_1 \oplus \dots \oplus G_k$.

If $G^- = \emptyset$, then G is a positive clique, since it is connected. Assume thus that $G^- \neq \emptyset$. Clearly, G^- must be discrete. Let $a \in G^-$. Assume that $v \in N_G(a)$ and $v, u \in G^+$ with $\{v, u\} \in E(G)$. Also $u \in N_G(a)$, since otherwise $\{a, v\}$ is a negative edge in $\text{gpr}_u(G)$. This shows that if $N_G(a) \cap G_i \neq \emptyset$, then $G_i \subseteq N(a)$.

Furthermore, G does not have an induced bipartite graph $K_{1,m}$ with at least three positive leaves. Indeed, if $v, u, w \in N_G(a)$ are not pairwise adjacent, then in $a, v, u \in \text{gpr}_w(G)^+$, and they are in the same connected component. However, $\{v, u\}$ is not an edge in $\text{gpr}_w(G)$ and so, $\text{gdr}_{v,u}$ will be applicable to $\text{gpr}_a(\text{gpr}_w(G))$; a contradiction. Consequently, any negative vertex is connected to at most two positive cliques in G .

Finally, suppose that there exist $a \in G^-$ and $u \in G^+$ such that $\{a, u\} \notin E(G)$. Since G is connected, there is a path from a to u in G . Choose a and u so that their path distance is as small as possible, and let such a shortest path be $a \rightarrow v \rightarrow \dots \rightarrow b \rightarrow u$, where $v \in G^+$ and $b \in G^-$. By the minimality assumption on a and u , we have $\{b, v\} \in E(G)$, and thus the vertices a, v, b, u induce a path P_4 . But now $\text{gpr}_b(\text{gpr}_u(G))$ contains the negative edge $\{a, v\}$; a contradiction. Hence a is connected to each vertex of G^+ , and consequently G^+ consists of at most two cliques. This proves the first part of the claim.

For the complexity part, note that if G^+ is a clique, then $\text{gpr}_v(G)$, for any $v \in G^+$, is a disjoint union of a positive clique and a discrete negative graph. Here $\mathcal{C}(\text{gpr}_v(G)) \leq 2$. On the other hand, if G^+ is a disjoint union of two cliques and v and u are in different components of G^+ , then gpr_v and gpr_u can be applied in parallel to G and $\text{gpr}_v \text{gpr}_u(G)$ is a discrete negative graph which is reducible in one parallel step. \square

Theorem 5.3. *A signed graph G has no reductions using double operations if and only if the connected components of G are double-split graphs where the negative vertices form the stable set.*

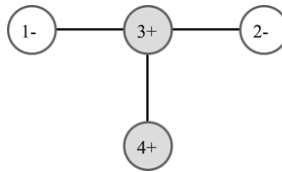


Fig. 3. A signed graph with no parallelism in any step of any reduction.

Proof. This is now clear from the proof of the previous lemma and by the fact that if G is of the stated form, so is $\text{gpr}_v(G)$ for all positive $v \in G^+$. \square

A related question is to determine which graphs avoid one type of operation in *at least one* strategy, rather than in all strategies. For the positive rules, the answer is the same as in Lemma 5.1. In the case of the negative and double rules, the problem remains open. However, the case for the negative rules leads to a problem of independent interest. The question is formulated in Problem 4 in a more general form. Note that this invariant result holds in a stronger form for signed double-occurrence strings, see [9] (for realistic strings), [3,4].

Problem 4. Is it true that the number of negative rules (gnr_v with $v \in G$) does not depend on the chosen reduction strategy for a given signed graph G ?

6. Graphs with no parallelism in the first step

A different approach to find high complexity signed graphs is to consider graphs for which no two operations can be applied in parallel, at least in the first step of any reduction.

The following result is clear from Theorem 3.2 and Example 2.

Lemma 6.1. Let G be a signed graph.

- (i) G has no two parallel applications of negative rules if and only if G has at most one isolated negative vertex.
- (ii) G has no two parallel applications of gpr -rules if and only if G^+ is a clique. Moreover, if G is positive, then $\mathcal{C}(G) \leq 2$.

An induced subgraph H of a (signed) graph G is a *shadow* of a vertex set (or a subgraph) $A \subseteq G$ if for each $x \in A$ and each edge $\{v, u\}$ of H , x is adjacent to v or u or both, and each isolated vertex of H is adjacent to a vertex in A .

Theorem 6.2. Let G be a signed graph of at least two vertices. Then G has no parallel applications of the rules (gnr , gpr , and gdr) if and only if

- (i) G^+ is a clique,
- (ii) G^- is a shadow of G^+ , and
- (iii) G^- consists of a discrete graph and a complete tripartite graph.

In this case, if G is negative or positive, then $\mathcal{C}(G) \leq 2$.

Proof. Suppose no two rules can be applied in parallel to G . Condition (i) follows from Lemma 6.1 and condition (ii) obviously holds since no rule gpr_v can be applied in parallel with a gnr_u or with a gdr_e . Condition (iii) follows from Corollary 4.2. The claim for the complexity for the cases $G = G^+$ and $G = G^-$ is clear.

The converse claim is equally clear. \square

The following simple example shows that the complexity claim of the previous theorem does not hold if the graph is not uniformly signed.

Example 3. The graph in Fig. 3 satisfies the conditions of Theorem 6.2. However, its parallel complexity is three. Note that this graph admits no two operations applied in parallel at any step of any reduction.

A further problem is to find those signed graphs that admit no two rules in parallel at any step of any reduction. With such a strong condition, our investigations so far show that only small graphs satisfy it.

Problem 5. Characterize the graphs for which the set of parallel reductions is identical with the set of sequential reductions.

7. Negative bipartite graphs of complexity one

In this section we consider the problem of characterizing those graphs G that have parallel complexity one. Not surprisingly, the problem is difficult to answer in general: it is equivalent to the older open problem of characterizing the negative graphs to which a given set of double rules may be applied in parallel [12], see also [Problem 1](#). We give a complete answer in several forms in this section for negative bipartite graphs. This is sufficient for the proof in the next section that negative trees have complexity at most two.

Recall that a signed graph $G = (V, E, \sigma)$ is (A, B) -bipartite, if A and B are stable sets in G forming a partition of V .

Lemma 7.1. *Let G be a negative (A, B) -bipartite graph with $A = \{a_1, \dots, a_n\}$ and $B = \{b_1, \dots, b_n\}$, such that $\{a_i, b_i\} \in E(G)$ and $N_G(a_i) \subseteq \{b_1, \dots, b_i\}$ for all $1 \leq i \leq n$. Then $M = \{\text{gdr}_{a_i, b_i} \mid 1 \leq i \leq n\}$ can be applied in parallel to G . Therefore $\mathcal{C}(G) = 1$.*

Proof. We prove the claim by induction on the order of the graphs. The result clearly holds for $n = 1$. Therefore assume that $n > 1$.

For each i , the graph $G_i = \text{gdr}_{a_i, b_i}(G)$ is bipartite. Indeed, $N_G(a_i) \subseteq B$ and $N_G(b_i) \subseteq A$, and hence no edges are created inside $A \setminus \{a_i\}$ or $B \setminus \{b_i\}$. Moreover, for any new edge $\{a_j, b_k\} \in E(G_i) \setminus E(G)$, we have $k \leq j$. Indeed, $b_k \in N_G(a_i)$ and $a_j \in N_G(b_i)$ and so, $k \leq i \leq j$. Consequently, $\{\text{gdr}_{a_j, b_j} \mid 1 \leq j \leq n, j \neq i\}$ is applicable in parallel to G_i , for all $1 \leq i \leq n$. Hence, by definition, the set of operations M can be applied in parallel to G . \square

If $M \subseteq E(G)$ is a matching of G , then a cycle γ of G is said to be *alternating* (or *M -alternating*), if every other edge in γ belongs to M and every other edge does not.

Lemma 7.2. *Let M be a matching in the negative bipartite graph G such that $\text{gdr}_M = \{\text{gdr}_e \mid e \in M\}$ is applicable in parallel to G . Then G does not have M -alternating cycles.*

Proof. Let G be (A, B) -bipartite. Assume that $\gamma = e_1 f_1 \dots e_n f_n$ is a minimum length M -alternating cycle in G , where $e_i = \{a_i, b_i\} \in M$ with $a_i \in A$, $b_i \in B$, and $f_i \notin M$. Then γ is induced, i.e., there are no chords $\{a_i, b_j\} \in E(G)$ in γ . If $n = 2$, then $\gamma = e_1 f_1 e_2 f_2$ is a square C_4 , which contradicts [Theorem 3.2\(iii\)](#). Therefore $n \geq 3$. Then, for any $e \in M$, $\text{gdr}_e(G)$ contains an $(M \setminus \{e\})$ -alternating cycle of $2n - 2$ edges, and $M \setminus \{e\}$ is a matching that is applicable in parallel to $\text{gdr}_e(G)$. Thus the claim follows inductively on the order of the graph G . \square

Lemma 7.3. *Let G be a negative bipartite graph which is not discrete. If $\mathcal{C}(G) = 1$, then G has a leaf.*

Proof. Let G be (A, B) -bipartite. We can assume that G is connected. Let $\mathcal{C}(G) = 1$. Therefore there exists a perfect matching $M \subseteq E(G)$ such that $\text{gdr}_M(G) = \emptyset$. Suppose that G does not have any leaves. Let $\{a_1, b_1\} \in M$ with $a_1 \in A$ and $b_1 \in B$. Since b_1 is not a leaf, there exists an edge $\{a_2, b_1\} \in E(G) \setminus M$ and $\{a_2, b_2\} \in M$ for some $b_2 \in B$, since $\text{gdr}_M(G) = \emptyset$. Proceeding inductively we obtain an M -alternating cycle in G which contradicts [Lemma 7.2](#). \square

Theorem 7.4. *Let G be a negative (A, B) -bipartite graph. Then $\mathcal{C}(G) = 1$ if and only if there are orderings $A = \{a_1, \dots, a_n\}$ and $B = \{b_1, \dots, b_n\}$ such that $\{a_i, b_i\} \in E(G)$ and $N_G(a_i) \subseteq \{b_1, \dots, b_i\}$, for all $1 \leq i \leq n$.*

Proof. The condition was proved necessary in [Lemma 7.1](#). For the reverse implication, note first that the claim is trivial for $n = 1$. Let then $n > 1$, and suppose that G has a perfect matching $M \subseteq E(G)$ so that $\text{gdr}_M(G) = \emptyset$.

By [Lemma 7.3](#), G has a leaf v . Let $u \in G$ be the unique vertex such that $e = \{v, u\} \in E(G)$. Then necessarily $e \in M$, and also $\mathcal{C}(G - \{v, u\}) = 1$. By the induction hypothesis, $G - \{v, u\}$ has orderings $A' = \{a_1, \dots, a_{n-1}\}$, $B' = \{b_1, \dots, b_{n-1}\}$ as claimed in the theorem. Now, if $v \in A$, then let $a_0 = v$, $b_0 = u$ and if $v \in B$, then let $a_n = v$, $b_n = u$. Clearly, these orderings satisfy the claim of the theorem. \square

Corollary 7.5. *Let G be a negative bipartite graph with $2n$ vertices, of parallel complexity one. Then*

- (i) G has at least two leaves, one in both partitions;
- (ii) G has at most $n(n+1)/2$ edges.

We can also now characterize the bipartite graphs with parallel complexity one in terms of alternating cycles.

Theorem 7.6. *A negative bipartite graph G has parallel complexity one if and only if G has a perfect matching without alternating cycles.*

Proof. Suppose $\mathcal{C}(G) = 1$, and thus that G has a perfect matching M such that for $\text{gdr}_M = \{\text{gdr}_e \mid e \in M\}$, we have $\text{gdr}_M(G) = \emptyset$. Now Lemma 7.2 gives the claim: there are no M -alternating cycles in G .

In converse, suppose that G has a perfect matching M such that G has no M -alternating cycles. It follows that for each edge $e \in M$, we have $M \setminus \{e\} \subseteq E(\text{gdr}_e(G))$, and thus $N = M \setminus \{e\}$ is a perfect matching of $\text{gdr}_e(G)$. We show that $\text{gdr}_e(G)$ has no N -alternating cycles. The claim follows from this by induction on the order of the graphs.

Suppose $H = \text{gdr}_e(G)$ does have an alternating cycle $\gamma = e_1 f_1 e_2 f_2 \dots e_n f_n$, where $e_i = \{a_i, b_i\} \in N$ for $i = 1, 2, \dots, n$. Let also $a_{n+1} = a_1$. Then there exists an edge $f_i = \{b_i, a_{i+1}\} \in E(H)$ such that $f_i \notin E(G)$, since γ is not a cycle in G , and $N \subseteq M$. Therefore $e = \{v, u\}$ and there are edges $\{v, a_{i+1}\}, \{u, b_i\} \in E(G)$. In G there is thus the path $\{b_i, u\}e\{v, a_{i+1}\}$, and since G does not have M -alternating cycles, there must be another edge $f_j = \{b_j, a_{j+1}\} \notin E(G)$. We can assume that $j < i$ and that $f_k \in E(G)$ for all k with $j < k < i$. However, if $\{v, a_{j+1}\} \in E(G)$, then $\{v, a_{j+1}\}e_{j+1} \dots e_i \{b_i, u\}e$ is an M -alternating cycle in G , and if $\{u, a_{j+1}\} \in E(G)$, then $\{u, a_{j+1}\}e_j \dots e_i \{b_i, v\}$ is a cycle of odd length in G . The latter case will not occur because G is bipartite. Hence $\text{gdr}_e(G)$ has no N -alternating cycles and this proves the claim. \square

From Theorems 7.6 and 7.4, we deduce

Theorem 7.7. *A negative bipartite graph G has parallel complexity one if and only if G has a unique perfect matching.*

Proof. Let G be (A, B) -bipartite for $A = \{a_1, \dots, a_n\}$ and $B = \{b_1, \dots, b_n\}$ as in Theorem 7.4, and let M be any perfect matching of G . Then $\{a_1, b_1\} \in M$, since $N_G(a_1) = \{b_1\}$. If $\{a_i, b_i\} \in M$ for all $i < j$, then also $\{a_j, b_j\} \in M$, since $N_G(a_j) \subseteq \{b_1, b_2, \dots, b_j\}$ and the vertices b_1, \dots, b_{j-1} have already been matched. This proves the uniqueness.

In converse, if M is a perfect matching of G and there is an M -alternating cycle $\gamma = e_1 f_1 e_2 f_2 \dots e_n f_n$, where $e_i = \{a_i, b_i\} \in M$, then also

$$N = (M \setminus \{e_1, e_2, \dots, e_n\}) \cup \{f_1, f_2, \dots, f_n\}$$

is a perfect matching. Hence if G has a unique perfect matching M , then G has no M -alternating cycles, and so $\mathcal{C}(G) = 1$ by Theorem 7.6. \square

For graphs that are not bipartite, the claim is not true. To see this, we can take the clique $G = K_{2n}$.

Corollary 7.8. *A non-discrete negative tree has parallel complexity one if and only if it has a perfect matching.*

8. Complexity of trees

8.1. Negative trees

We prove in this section that any negative tree can be successfully reduced in parallel in two steps.

The following lemma is clear from the definition of the double rule.

Lemma 8.1. *Let $e = \{a, b\}$ be an edge of $\text{gdr}_{v,u}(G)$ that is not an edge of G . Then $\{a, b\} \cup \{v, u\}$ induces a path P_4 in G .*

Recall that an edge $e \in E(G)$ is a *bridge*, if the removal of e disconnects G . An edge is a bridge if and only if it belongs to no cycle of G ; see e.g. [23]. In the following lemma we show that bridges are inherited by the double rules.

Lemma 8.2. *Let $e = \{a, b\}$ be a bridge in G . Then e is a bridge of $\text{gdr}_{v,u}(G)$ for each edge $\{v, u\} \in E(G)$, where $v, u \notin \{a, b\}$.*

Proof. Let $H = \text{gdr}_{v,u}(G)$. Since $e = \{a, b\} \in E(G)$ is a bridge and $\{v, u\} \in E(G)$, it is clear that $\{a, b\} \not\subseteq N_G(v) \cup N_G(u)$, for otherwise $\{a, b, v, u\}$ gives a cycle in G . Hence $e \in E(H)$. Suppose then that e is not a bridge in H . Then there exists a path in H from a to b that does not contain e . If an edge f on this path does not belong to G , then by Lemma 8.1, the ends of f are still connected by a path of length four in G . From this it follows that there is a connecting path of a and b in G that does not use the edge e ; a contradiction. \square

Lemma 8.3. *For any negative graph G , if M is a matching of G consisting of bridges only, then gdr_M is applicable in parallel to G .*

Proof. By Lemma 8.2, for each edge $e \in M$, we have that $M \setminus \{e\}$ is a matching of $\text{gdr}_e(G)$ also consisting of bridges only. Consequently, gdr_M can be applied sequentially and in any order on the edges of M . Thus gdr_M is applicable in parallel to G . \square

Let M be a matching of a graph G . We say that a path $P = e_1 e_2 \dots e_m$ is M -alternating, if $e_{2i-1} \notin M$ and $e_{2i} \in M$ for all $i \geq 1$. Such a path P is M -augmented, if the ends of the path are not saturated by M , i.e, if the path starts from a and ends in b , then a and b are not endpoints of any edge $e \in M$.

Theorem 8.4. *Let M be a maximum matching of a negative graph consisting only of bridges of G . Then $\text{gdr}_M(G)$ is discrete.*

Proof. First of all, $\text{gdr}_M(G)$ does not have any edges of G , since M is maximum, and the ends of the edges in M are removed from G . Let $M = \{e_1, e_2, \dots, e_m\}$, and denote $G_0 = G$ and $G_i = \text{gdr}_{e_i}(G_{i-1})$ for all $i = 1, 2, \dots, m$. Suppose that $\{v, u\}$ is an edge in G_i but not in G_{i-1} . Hence $\{v, u\}$ is created by applying gdr_{e_i} to G_{i-1} for $e_i = \{a, b\} \in M$, and so there is an M -alternating path in G_{i-1} from v to u . Indeed, this path is either (v, a, b, u) or (v, b, a, u) . Inductively, we obtain that there is an M -alternating path in G_j from v to u for each $j < i$, and therefore also in G . We conclude that one of the ends, v or u , must be saturated by M by Berge's criterion for maximum matchings; see [23]. The claim follows from this by applying the above to the final result $G_m = \text{gdr}_M(G)$ \square

Corollary 8.5. *Any negative tree can be reduced in one step to a discrete graph and so, its complexity is at most two.*

8.2. Positive trees

In this section we prove that any positive tree can be reduced in one step to a negative graph that may not be a tree anymore. However, we are able to prove that these graphs have a special form and in particular, they have complexity at most two.

The following purely graph theoretic result is interesting on its own.

Lemma 8.6. *Every tree T has a stable set I such that the vertices $v \notin I$ are adjacent to an odd number of elements of I .*

Proof. The proof goes by induction on the number of vertices in the tree. The claim is clear for trees of size at most 4. Suppose the claim holds for all trees of at most $n - 1$ vertices. Let T be a tree of n vertices. We divide the proof to several cases that exhaust all possibilities.

We say that a subset $I \subseteq T$ is *good* if I is stable and each $v \in G \setminus I$ is adjacent to an odd number of elements of I .

(1) Assume T has a vertex v adjacent to at least two leaves, say x and y . Consider the subtree $T' = T - \{x, y\}$ which has, by the induction hypothesis, a good subset I' . If $v \in I'$, then clearly $I = I'$ is a good subset of T , since x and y are adjacent in T to only one element of I , namely v . On the other hand, if $v \notin I'$, then $I = I' \cup \{x, y\}$ is a good subset of T , since it is stable and since v is adjacent to an even number (two) new neighbors, not in I' .

There remains the case where each vertex of T is adjacent to exactly one leaf or no leaves at all. A path v_1, v_2, \dots, v_k is called a *branch*, if v_k is a leaf and $\deg(v_i) = 2$ for $i = 2, \dots, k - 1$. (The vertex v_1 can have more neighbours in T .)

(2) Suppose first that T has a long branch v_1, v_2, \dots, v_k for some $k \geq 4$. The induction hypothesis applied to the subtree $T' = T - \{v_{k-2}, v_{k-1}, v_k\}$ gives a good subset I' of T' . If $v_{k-3} \in I'$ then $I = I' \cup \{v_k\}$ is good for T , and if $v_{k-3} \notin I'$ then $I = I' \cup \{v_{k-1}\}$ is good for T .

(3) Hence we can assume that the branches are all of length $k \leq 3$. In this case there exists a vertex $v \in T$ such that v starts at least two branches and the degree of v is $|N_T(v)| \geq 3$.

(3.1) Suppose first that there are different branches v, x_1, x_2 and v, y_1, y_2 both of length two. By the induction hypothesis, the subtree $T' = T - \{x_1, x_2\}$ has a good subset I' . Now $v \notin I'$, since otherwise $y_1 \notin I'$ and so also $y_2 \notin I'$ contradicting the fact that y_2 is adjacent to an element of I' . Therefore, $I = I' \cup \{x_2\}$ is good for T .

(3.2) Finally suppose that there are different branches v, x_1 and v, y_1, y_2 . By the induction hypothesis $T' = T - \{x_1\}$ has a good subset I' . As in the previous case $v \notin I'$. In this case, either $y_1 \in I'$ or $y_2 \in I'$. If $y_1 \in I'$, then $y_2 \notin I'$, and $I = (I' \setminus \{y_1\}) \cup \{x_1, y_2\}$ is good for T . On the other hand, if $y_2 \in I'$ and so $y_1 \notin I'$, then $I = (I' \setminus \{y_2\}) \cup \{x_1, y_1\}$ is good for T . This proves the claim. \square

We say that a stable subset $I \subseteq T$ is a *signer subset* for the positive tree T if $\text{gpr}_I(T)$ is a negative graph. Note that $\text{gpr}_I(T)$ need not be a tree.

Lemma 8.7. *Let T be a positive tree. Then it has a signer subset $I \subseteq T$. Moreover, if I is a signer subset, then $\text{gpr}_I(T)$ can be reduced to a discrete graph in one parallel step.*

Before proving Lemma 8.7, we need to state two auxiliary results about all-negative graphs.

Lemma 8.8. *Let G be an all-negative graph and u, v twins in G . Then*

- (i) *u and v are twins in every $\text{gdr}_{x,y}(G)$, whenever $u, v \notin \{x, y\}$, and*
- (ii) *$\text{gdr}_{u,v}(G) = G \setminus \{u, v\}$.*

Lemma 8.9. *Let G be an all-negative graph, K a clique of G and $u_0 \in K$ the only vertex of K adjacent to vertices in $G \setminus K$.*

- (i) *For any edge vw of K , $u_0 \notin \{v, w\}$, $\text{gdr}_{v,w}(G) = G \setminus \{v, w\}$;*
- (ii) *For any edge xy in $G \setminus K$, K is a clique in $\text{gdr}_{x,y}(G)$ and u_0 is the only vertex of K adjacent to vertices in $\text{gdr}_{x,y}(G) \setminus K$;*
- (iii) *For any edge u_0v of K , $K \setminus \{u_0, v\}$ is a clique in $G' = \text{gdr}_{u_0,v}(G)$ and for all $u \in K \setminus \{u_0, v\}$, $N_{G'}(u) \cup \{u\} = N_G(u_0) \setminus \{v\}$;*
- (iv) *For any edge u_0x of G , with $x \notin K$, $K \setminus \{u_0\}$ is a clique in $G'' = \text{gdr}_{u_0,x}(G)$ and for all $u \in K \setminus \{u_0\}$, $N_{G''}(u) \cup \{u\} = N_G(x) \cup (K \setminus \{u_0\})$.*

Proof of Lemma 8.7. If I is a stable subset of T , then $\text{gpr}_I = \{\text{gpr}_v \mid v \in I\}$ can be applied in parallel to T , and so $G = \text{gpr}_I(T)$ is well defined. By Lemma 8.6, there exists a stable subset $I \subseteq T$ such that each $v \notin I$ has an odd number of neighbors in I . Therefore each sign $v \in T$ is changed to negative in $\text{gpr}_I(T)$, and hence $G = \text{gpr}_I(T)$ is a negative graph. Hence I is a signer subset of T .

For the second part of the theorem, let $I = \{v_1, \dots, v_m\}$ be a signer subset of T . Since T is a tree, the neighborhood $K_i = N_G(v_i)$ of each $v_i \in I$ is a stable set, and thus it induces a clique in G . Moreover, in order to avoid cycles in T , we must have that $|K_i \cap K_j| \leq 1$ for all different i and j . In case $K_i \cap K_j = \emptyset$, there is at most one pair of vertices $v \in K_i, u \in K_j$ with $\{v, u\} \in E(G)$, since in this case also $\{v, u\} \in E(T)$. In all such cases, we add to our list of cliques the clique $\{u, v\}$. Let $K_1, \dots, K_n, n \geq m$ be our final list of cliques, where there is no edge between vertices in distinct cliques.

Observe now that there are no distinct vertices $u_1, \dots, u_k, k \geq 3$, such that $u_l \in K_{i_l} \cap K_{i_{l+1}}, 1 \leq l \leq k-1$, and $u_k \in K_{i_k} \cap K_{i_1}$, for some $1 \leq i_1, \dots, i_k \leq n$. We say that the cliques K_1, \dots, K_m induce a forest-like ‘meta-structure’ in the following formal sense: (i) the cliques K_1, \dots, K_n are intersecting on at most singletons, and (ii) all simple cycles of G are simple cycles of some clique $K_j, 1 \leq j \leq n$.

We prove the claim of the lemma by induction on the number of vertices in the graph, for all graphs that are forest-like, as defined above.

For the inductive step, note that it follows directly from the definition of forest-like that there is a clique, say K_1 , that is a ‘leaf’ in our meta-structure: there is at most one vertex $u_0 \in K_1$ such that $u_0 \in K_i$, for some $i \neq 1$. If K_1 has no such vertex u_0 (i.e., K_1 is ‘isolated’), then applying gdr on any maximal matching for K_1 will reduce K_1 to a discrete graph, and it may be applied in parallel with any other gdr operations applied on edges of $G \setminus K_1$. Assume now that K_1 is not ‘isolated’ in G .

If $|K_1| = 2$, say $K_1 = \{u_0, v\}$, then observe that $G \setminus K_1$ has a forest-like ‘meta-structure’ and so, by induction hypothesis, there is a matching M' of $G \setminus K_1$ such that $\text{gdr}_{M'}(G \setminus K_1)$ is a discrete graph. We claim that gdr is applicable in parallel on $M = M' \cup \{u_0v\}$ to G and $\text{gdr}_M(G)$ is discrete. To this aim, we must show that gdr operations may be applied in any sequential order on edges in M . Note first that based on Lemma 8.9, throughout applying gdr operations on edges in M' , K_1 remains a clique, with u_0 its only vertex adjacent to vertices outside K_1 . Consequently, gdr may be applied on u_0v at any point, resulting only in the removal of vertices u_0 and v . Then gdr may be applied on the remaining edges of M' in an arbitrary order, proving the claim.

If $|K_1| > 2$, then let $u, v \in K_1 \setminus \{u_0\}$. Observe that $G \setminus \{u, v\}$ has a forest-like ‘meta-structure’ and so, by induction hypothesis, there is a matching M'' of $G \setminus \{u, v\}$ such that $\text{gdr}_{M''}(G \setminus \{u, v\})$ is a discrete graph. We claim that gdr is applicable in parallel on $M = M'' \cup \{uv\}$ to G and $\text{gdr}_M(G)$ is discrete. It follows from our choice of u, v that $N_G(u) \cup \{u\} = N_G(v) \cup \{v\}$. Consequently, based on Lemmas 8.8 and 8.9, throughout applying gdr operations on any edges of M'' , the edge uv is preserved and their closed neighborhoods remain the same. Thus, $\text{gdr}_{u,v}$ is applicable at any point, resulting only in the removal of u, v . Then gdr may be applied on the remaining edges of M'' in an arbitrary order, proving the claim. \square

9. Discussion

Although the parallel complexity of negative and positive trees is bounded, the question of the bound for that of the signed trees still remains open. The reason is that by local complementing, a signed tree may be transformed into an arbitrary graph. The following table lists the smallest signed trees with respect to the complexity from one to five. The result is based on a full search that explores all possible signed trees of less than 18 vertices. Here, n is the size of the tree, \mathcal{C} is the parallel complexity corresponding to the tree. See examples and proofs in [14].

\mathcal{C}	1	2	3	4	5
n	1	2	3	6	12

Since there is no known efficient way to decide the maximum set of negative edges that can be reduced in parallel for a given set of edges S in a given graph G , a bound on the parallel complexity for negative graphs is not concluded. Here, we recall the conjecture in [12], that negative graphs only have parallel complexity up to three. Indeed, it is possible to find negative graphs of parallel complexity three, while negative graphs of complexity higher than that is not found through an automated search [24]. Interestingly, the negative graphs found of parallel complexity three are tripartite graphs [14].

Settling the complexity of positive graphs seems to be a difficult problem. The main reason for this is that this class of graphs is not closed under gpr . Some positive tripartite graphs of parallel complexity four have been reported in [14], the highest complexity currently known for this class.

Graphs with parallel complexity up to six were reported in [14]. Proving the complexity of those graphs is based essentially on a computer-based exhaustive search implemented in [24], see [15] for a description of the algorithm.

Acknowledgment

The authors gratefully acknowledge support by Academy of Finland (TH – project 39802, CL – project 203667, IP – project 108421).

References

- [1] A. Bouchet, Circle graphs, *Combinatorica* 7 (1987) 243–254.
- [2] A. Bouchet, Circle graph obstructions, *J. Combin. Theory Ser B* 60 (1994) 107–144.
- [3] R. Brijder, H.J. Hoogeboom, G. Rozenberg, Reducibility of gene patterns in ciliates using the breakpoint graph, *Theoret. Comput. Sci.* 356 (2006) 26–45.
- [4] R. Brijder, H.J. Hoogeboom, M. Muskulus, Strategies of loop recombination in ciliates, *Discrete Appl. Math.* (2007).
- [5] A. Fleury, F. Delgado, A. Adoutte, Molecular phylogeny of ciliates: What does it tell us about the evolution of the cytoskeleton and of developmental strategies? *Dev. Genet.* 13 (1992) 247–254.
- [6] A. Ehrenfeucht, T. Harju, I. Petre, D.M. Prescott, G. Rozenberg, *Computation in Living Cells: Gene Assembly in Ciliates*, Springer, 2004.
- [7] A. Ehrenfeucht, D.M. Prescott, G. Rozenberg, Computational aspects of gene (un)scrambling in ciliates, in: L.F. Landweber, E. Winfree (Eds.), *Evolution as Computation*, Springer, Berlin, Heidelberg, New York, 2001, pp. 216–256.

- [8] A. Ehrenfeucht, T. Harju, I. Petre, G. Rozenberg, Characterizing the micronuclear gene patterns in ciliates, *Theory Comput. Syst.* 35 (2002) 501–519.
- [9] A. Ehrenfeucht, D.M. Prescott, G. Rozenberg, Circularity and other invariants of gene assembly in ciliates, in: M. Ito, Gh. Paun, S. Yu (Eds.) *Words, Semigroups, and Transductions*, World Scientific, Singapore, pp. 81–97.
- [10] A. Ehrenfeucht, D.M. Prescott, G. Rozenberg, Modelling gene assembly in ciliates, in: G. Ciobanu, G. Rozenberg (Eds.), *Modelling in Molecular Biology*, in: *Natural Computing Series*, Springer Verlag, 2004, pp. 105–124.
- [11] T. Harju, C. Li, I. Petre, G. Rozenberg, Parallelism in gene assembly, in: *Proceedings of the 10th International Meeting on DNA-Based computers DNA 10*, Milan, Italy, in: *Lecture Notes in Computer Science*, vol. 3384, 2005, pp. 140–150.
- [12] T. Harju, C. Li, I. Petre, G. Rozenberg, Parallelism in gene assembly, *Natural Comput.* 5 (2006) 203–223.
- [13] T. Harju, C. Li, I. Petre, G. Rozenberg, Complexity measures for gene assembly, in: *Lecture Notes in Bioinformatics (LNBI)*, vol. 4366, Springer, 2007.
- [14] T. Harju, C. Li, I. Petre, Parallel complexity of signed graphs for gene assembly in ciliates, in: *Soft Computing — A Fusion of Foundations, Methodologies and Applications*, 2008 (in press).
- [15] A. Alhazov, C. Li, I. Petre, An Algorithm for the parallel complexity of graph-based ciliate genes assembly (2007) (submitted for publication).
- [16] C.L. Jahn, L.A. Klobutcher, Genome remodeling in ciliated protozoa, *Ann. Rev. Microbiol.* 56 (2000) 489–520.
- [17] L.F. Landweber, L. Kari, The evolution of cellular computing: Nature’s solution to a computational problem, in: *Proceedings of the 4th DIMACS Meeting on DNA-Based Computers*, Philadelphia, PA, 1998, pp. 3–15.
- [18] L.F. Landweber, L. Kari, Universal molecular computation in ciliates, in: L.F. Landweber, E. Winfree (Eds.), *Evolution as Computation*, Springer, Berlin, Heidelberg, New York, 2002.
- [19] D.M. Prescott, The DNA of ciliated protozoa, *Microbiol. Rev.* 58 (2) (1994) 233–267.
- [20] D.M. Prescott, DNA manipulations in ciliates, in: W. Brauer, H. Ehrig, J. Jarhumäki, A. Salomaa (Eds.), *Formal and Natural Computing: Essays Dedicated to Grzegorz Rozenberg*, in: *LNCS*, vol. 2300, Springer, 2002, pp. 394–417.
- [21] D.M. Prescott, A. Ehrenfeucht, G. Rozenberg, Molecular operations for DNA processing in hypotrichous ciliates, *European J. Protistol.* 37 (2001) 241–260.
- [22] D.M. Prescott, A. Ehrenfeucht, G. Rozenberg, Template-guided recombination for IES elimination and unscrambling of genes in stichotrichous ciliates, *J. Theoret. Biol.* 222 (2003) 323–330.
- [23] D.B. West, *Introduction to Graph Theory*, Prentice Hall, Upper Saddle River, NJ, 1996.
- [24] Gene assembly simulator, <http://combio.abo.fi/simulator/simulator.php>. 2006.